

# Non-reciprocal Light-harvesting Antennae

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## Abstract

From a point of view of classical electrodynamics, the performance of two-dimensional shape-simplified antennae is discussed based upon the shape of naturally designed systems to harvest light. The modular design of nature is found to make the antenna non-reciprocal, hence more efficient. We further explain the reason that the light harvester must be a ring instead of a ball, the function of the notch at the LH1-RC complex, the non-heme iron at the reaction center, the chlorophylls are dielectric instead of conductor, a mechanism to prevent damages from excess sunlight, the functional role played by the long-lasting spectrometric signal observed, and the photon anti-bunching observed. Our model has the required structural information automatically built in. We comment about how our prediction might be verified experimentally.

*Keywords:* small-loop antenna, non-reciprocal antenna, dielectric resonator antenna, light harvester, electrodynamics, photosynthesis, LH1, LH2

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## 1. Introduction

Photosynthesis that occurs daily in bacteria, algae and plants has been a subject traditionally studied by chemists and biochemists[1, 2, 3, 4]. A major task in this field was trying to understand the molecular structures. Because of the inadequate instrumental resolution, people struggled for decades to know the structure of the light-harvesting antenna. Without precise structures, investigators tried to guess the content within the black box[5].

The Fenna-Matthews-Olson (FMO) complex of green sulfur bacteria was the first pigment-protein complex to have its structure analyzed with x-ray diffraction [6]. These bacteria live deep in the sediments of water; as they encounter only few photons per second[7], they hence require an efficient mechanism to harvest light. They consist of chlorosomes and the FMO complex that function together. The chlorosomes are the largest known photosynthetic complexes in existence, comprising about 250,000 pigment molecules. In contrast, the FMO

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complex that mediates the transfer of excitation energy from the light-harvesting chromosomes to the bacterial reaction center (RC) is a small trimeric structure (symmetry C3); each of the three monomers contains only seven bacteriochlorophyll *a* molecules.

In 1984, the first crystal structure of RC was determined, which resulted in a Nobel Prize four years afterward[8].

Beginning about 1995, scientists have acquired a reasonably complete picture of the bacterial light-harvesting (LH) system [9, 10, 11]. Both the inner antenna, LH1, and the outer antenna, LH2, are assembled from the same modules to form rings. Each module consists of two short  $\alpha$ -helical polypeptides coordinating one carotenoid and three bacteriochlorophylls. The exact numbers of modules involved for both complexes are variable [9, 12, 13]. The outer antenna, LH2, is smaller and consists of nine units for *Rhodospseudomonas acidophila* [14, 15] with inner diameter 36 Å and outer diameter 68 Å; But the inner antenna, LH1, is larger, as it contains the RC, and is composed of 16 units, for *Rhodospirillum rubrum* with outer diameter 116 Å and central diameter 68 Å [12].

Two further subtleties in the structure of LH1 are important. First, the ring has a mysterious opening[16]. Some earlier authors simply drew a misleading cartoon that propagated across succeeding generations[2, 17]. Second, the RC contained in the LH1 has a non-heme iron.

Many such structures have been subsequently analyzed[18], some of which we list in Table 1. At present, for only *Rhodospseudomonas palustris* is the x-ray crystal structure known for its LH1-RC complex. Symmetries are notably unaltered even under strained conditions for LH3, i.e., a variant of LH2[19].

Following a knowledge of the structure, a question remains. Why has a light harvester form a tambourine-like shape instead of a spherical shape or a serpentine shape, for instance? The number of modules involved is presumably unimportant; otherwise it would not vary from species to species.

Since 1948, Förster's theory has dominated the community to describe inter-molecular energy transfer because it contains mainly the experimentally accessible parameters[25]. In 1959, Duysens considered the efficiency of conversion of radiant energy from the second law of thermodynamics and showed that the maximum measurable efficiency of algae photosynthesis is less than 70%[26]. A model of classical random walks on lattices has also been applied to encompass the energy transfer amongst light-harvesting antennae[27]. Investigators in quantum physics have also been working on photosynthesis because of a question posed by Lee et al.[28]. They considered the remarkable efficiency of transfer within the FMO complex to be a kind of quantum search, but a consensus is a kind of quantum random walk[29, 30]. The same group further claimed that they obtained evidence for "wavelike energy transfer through quantum coherence"[31], which made some physicists consider photosystems as a quantum heat engine[32, 33]. In particular, they considered such an engine working under noisy conditions. These models, though physical, do not rely upon structural information.

We tried to put some structure into a model by calculating a simplified LH1 model based upon the chemical rate equations for the shape acquired, but

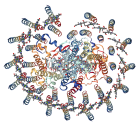
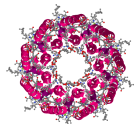

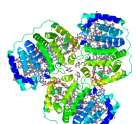
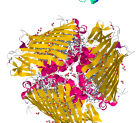

protein	PDB ID	symmetry	cartoon
LH1-RC from <i>Rhodopseudomonas palustris</i> [20]	1PYH		
LH2 B800-850 from <i>Rhodopseudomonas acidophila</i> [15]	1NKZ	C9	
LH2 B800-850 from <i>Rhodospirillum rubrum</i> [21]	1LGH	C8	
peridinin-chlorophyll from <i>Amphidinium carterae</i> [22]	1PPR	C3	
FMO from <i>Prosthecochloris aestuarii</i> [23]	3EOJ	C3	
allophycocyanin from cyanobacterium <i>Phormidium</i> [24]	4RMP	C3	

Table 1: Various light-harvesters with structural symmetry. PDB ID is the protein ID assigned by Protein Data Bank <http://www.rcsb.org/pdb/>

advanced no farther than others[34]. In the present work LH are considered from a classical electrodynamic point of view, as the light-harvesting antennae function the same as radio antennae from many perspectives except their size and their reception frequencies. Notably, our model automatically contains the required structural information. We can explain the function of the notch at the LH1-RC complex still unknown to biochemists, the function of the non-heme iron at the reaction center, some spectrometric observations, and much more. We show how classical physics instead of quantum physics is working for the major part of photosynthesis.

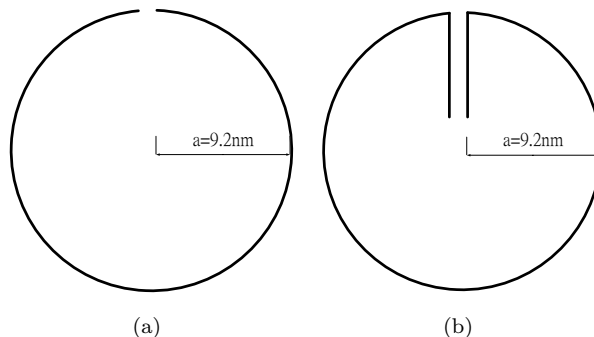


Figure 1: Antennae of two simplified shapes. According to experimental data, the radius is the average of  $68 \text{ \AA}$  and  $116 \text{ \AA}$ , which equals  $92 \text{ \AA}$ . (a) is called a loop antenna whereas (b) is called a loop antenna with line feed. Although resembling the special pair in the RC, the feed line modifies the resonance frequency only slightly, but the notch is essential.

## 2. Loop Antennae

Two simplified shapes are shown in the figure. Figure 1 (a) is simple and can be solved with algebraic methods, whereas figure 1 (b), although resembling LH1 more closely, has a resonance frequency only slightly modified from that of figure 1 (a). We must hence consider only figure 1 (a). The notch is essential for *LH1* as the received energy must be taken from some point. The *Rhodospseudomonas palustris* molecule of 1PYH shown in the table also has a notch.

In engineering, antennae of such shapes are well studied: they are called loop antennae and loop antennae with line feed, respectively[35]. Figure 1 (a) was used by Heinrich Hertz when he first demonstrated radio waves around 1888; the only difference is that the wavelength of our consideration is small, into the optical region.

Loop antennae divide into two categories depending upon their size relative to the wavelength of operation. If an antenna has a radius smaller than the wavelength of operation, it is called a small-loop antenna; otherwise it is called a resonant-loop antenna. As the wavelength,  $\lambda$ , of operation of LH1 or LH2,  $800 - 900 \text{ nm}$ , is much larger than the radius of the antenna,  $9.2 \text{ nm}$ , the light-harvesting antenna is a small-loop antenna, which has a small efficiency and serves mainly as a receiving antenna.

To arrive at the electromagnetic properties of such an antenna there are a complete way and a simple way. We begin with the complete way.

Let the radius of the loop located at the origin be  $a$ , and the plane of the loop be  $x - y$ ; let the angle from the  $x$ -axis be  $\phi$ . If current  $I$  around the loop is uniform and in phase, the only component of the vector potential is  $A_\phi$ , as shown in Figure 2 (a). The infinitesimal value of  $A_\phi$  at a point away from the

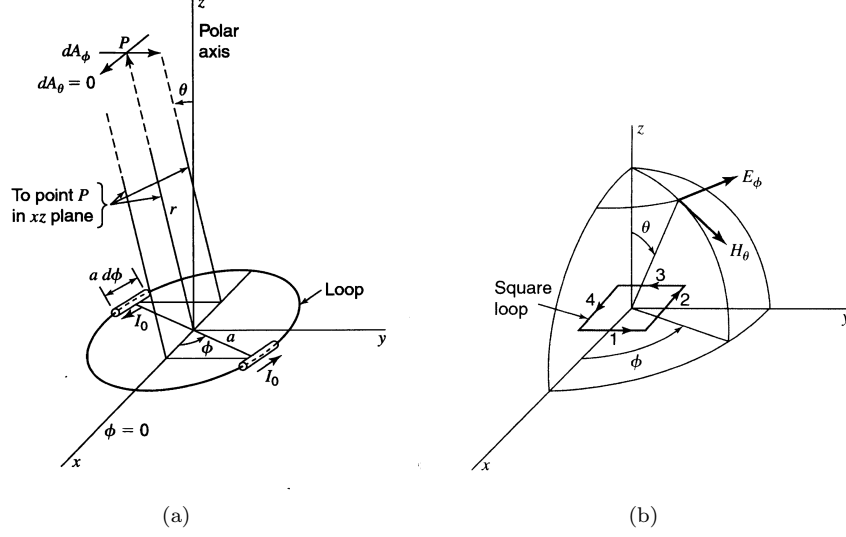


Figure 2: The coordinate system uses.

loop by distance  $r$  caused by two diametrically opposed infinitesimal dipoles is

$$dA_\phi = \frac{\mu dM}{4\pi r}, \quad (1)$$

in which  $dM = 2j[I]a \cos \phi [\sin(2\pi a \cos \phi \sin \theta / \lambda)] d\phi$ ,  $\theta$  is the angle relative to the vertical axis through the center of the loop, and  $[I] = I_0 \exp \{j\omega[t - (r/c)]\}$  is the retarded current on the loop with  $I_0$  being its maximum value. After integration we obtain

$$A_\phi = \frac{j\mu[I]a}{2r} J_1\left(\frac{2\pi a \sin \theta}{\lambda}\right), \quad (2)$$

in which  $J_1$  is a Bessel function of first order.

As the source of sunlight is remote, we consider the far-field effects. The far electric field of the loop has only a  $\phi$ -component  $E_\phi = -j\omega A_\phi$  that is in the plane of the loop. Therefore,

$$E_\phi = \frac{120\pi^2 a [I]}{\lambda r} J_1\left(\frac{2\pi a \sin \theta}{\lambda}\right). \quad (3)$$

The corresponding magnetic field in free space is

$$H_\theta = \frac{\pi a [I]}{\lambda r} J_1\left(\frac{2\pi a \sin \theta}{\lambda}\right). \quad (4)$$

The second method is to decrease the infinite number of dipoles used in the preceding method into four short linear dipoles as follows.

Let the area of the antenna be  $A$ , which is commonly called the aperture of the antenna, and the length of the dipoles be  $d$ , as shown in Figure 2 (b). Hence

$$d^2 = \pi a^2 \equiv A \quad (5)$$

The far electric field is

$$E_\phi = \frac{120\pi^2[I] \sin \theta}{r} \frac{A}{\lambda^2}. \quad (6)$$

The term  $A/\lambda^2$  is a pure ratio: it is the aperture in terms of wavelength. The magnetic field is obtained on dividing the intrinsic impedance of the medium, i.e.

$$H_\theta = \frac{E_\phi}{120\pi} = \frac{\pi[I] \sin \theta}{r} \frac{A}{\lambda^2} \quad (7)$$

in vacuum.

Eq. (6) is a special case of Eq. (3), just as Eq. (7) is a special case of Eq. (4), as for small arguments of the first-order Bessel function  $J_1(x) \approx x/2$ .

The (radiation or receiving) resistance at the loop terminals can be obtained from

$$P = \frac{I_0^2}{2} R \quad (8)$$

in which  $I_0$  is the maximum current on the loop and  $R$  is the resistance. The total power  $P$  is obtainable on integrating the Poynting vector

$$S = \frac{1}{2} |H|^2 \text{Re}Z \quad (9)$$

over a large sphere, in which  $Z$  is the impedance of the medium. The resistance thus obtained for a small-loop antenna is proportional to  $1/\lambda^4$ .

Antennae are generally constructed of size about  $\lambda/4$ . As the size decreases, the terminal impedance (complex resistance) becomes increasingly reactive, which hinders the transfer of power; the coupling between the circuit and the wave becomes unsatisfactory.

### 3. Non-reciprocal Antennae

A regular antenna both receives and emits, because Maxwell's equations are symmetric with respect to time reversal[36], but a light harvester that functions solely as a receiver must receive much better than it emits. What we seek is more than an optical equivalent of an electronic rectifier, which is artificial, but an optical counterpart of a duckbill check valve in fluid dynamics. Such a valve is a naturally designed passive device that exists in a human heart. In particular, these atrioventricular valves include the mitral valve and the tricuspid valve, and semilunar valves.

As no modal or polarization properties of sunlight are known, we require mechanisms to break the (Lorentz) time-reversal symmetry[37]. There are several possibilities to make such an optical check valve:

- Faraday rotator[38, 39];
- circulator[36, 40];
- duplexer[41, 42, 43];
- nonlinearity [44, 45, 46, 47, 48, 49].

All four mechanisms are well known to the scientific and engineering communities.

- The first mechanism, a Faraday rotator, requires an externally applied magnetic field. All LH1-RC complexes are equipped with a non-heme iron at the RC, i.e. the *Rhodobacter sphaeroides* RC[50], which could provide the required field. The iron is not bound to any protein and can be exchanged with zinc ( $Zn^{2+}$ ) or manganese ( $Mn^{2+}$ ), just like a pearl in a mussel's mouth that chemists call "coordinated"[51, 52, 53, 54]. The role played by the non-heme iron has long been questioned, if not unknown to biochemists[55]. Biologists know that it serves as a source or sink of electrons during electron transfer or redox chemistry, without recognizing the implication of magnetic fields[56]. The fact that the non-heme iron can be exchanged confirms our prediction about the role played by the iron. Presumably, it can also be exchanged with other magnetic atoms.

The effect is, however, typically small and decreases proportionally to  $\lambda^{-2}$  in an organic material, although there are isolated reports of large Faraday rotation[57, 58]. In contrast, a nano-scale (quantum) optical isolator (circulator) that requires neither great intensity of light nor a strong magnetic field but relies upon polarization has been built [59, 40].

Furthermore, although the main concern of the present paper is a bacterial light harvester, molecular data show that photosystems of algae and plants likely evolved from the photosystems of green-sulfur bacteria; there are hence many analogous functions and similar structures. The photosystems (I and II) of algae and plants are not only typically equipped with non-heme iron but even manganese ( $Mn$ )[60, 61].

- The geometry of the second mechanism, a circulator, resembles our LH well. The FMO complex is a 3-port circulator; *Rhodospseudomonas acidophila* LH2 (PDB ID 1NKZ and 1KZU) is a 9-port circulator, whereas LH1 for *Rhodospirillum rubrum* is a 16-port circulator. Such optical circulators are commonly used in fibre-optic transmission to direct the optical signal from one port to another port and in only one direction.
- Duplexer (or multiplexer) is the term used in communication engineering, whereas physicists use the descriptor time-dependent material, which might function together with the circulator. Biochemists know that, when a chlorophyll pigment absorbs light, it loses an electron to the RC, which might also mean duplexing [3]. Interpreted in terms of mechanics, the

photon received might cause the  $\alpha$ -helical polypeptides/ carotenoid/ bacteriochlorophyll complex to alter its shape or orientation, hence rendering impracticable the flow of the electromagnetic wave in the other direction. Theorists have previously remarked that the FMO complex might work as a rectifier for unidirectional energy flow without specifying how that action proceeds[62]. With this mechanism the near-unity quantum efficiency of conversion is not peculiar because the electron has been locked in[63].

The wave-like energy transfer or the coherence at room-temperature observed by previous authors might simply signify a collective motion (mechanical movement) instead of quantum coherence[31], as light at this wavelength, in comparison with the size of the antenna, should be considered as a wave instead of a particle. The functional role played by the persistent spectrometric signal observed might simply mean duplexing, as discussed here. The chlorophylls move in unison with the light wave as seaweed moves with the tides. A recent finding of photon anti-bunching from LH supports such a scenario, although no further reason for the physics behind conformational change was provided[64, 65].

Current methods of imaging with a microscope not only are limited by the wavelength used but also require harsh conditions or direct mechanical interaction with the samples, hence becoming inappropriate for live cells. A newly invented imaging method using phonons (acoustic waves) of sub-optical wavelength or a photonic crystal-enhanced microscope might enable one to observe the route that a photon takes on entering and leaving LH, to discover how the LH alters its conformation[66, 67]. Otherwise, we might be able to fabricate a nano-scale optical isolator, by chemical or biological synthesis for example, according to scaling laws, to assess whether it generates spectra of the same characteristics as a real light harvester[68, 69]. The molecule thus synthesized need not be organic, or even light-sensitive, as what we are considering is the geometric effect.

- Fourthly, the LH are apparently nonlinear media. The internal quantum states of the non-heme iron at the RC can serve to control the direction of the light propagation[40].

The above statements have not excluded a spherical shape, which occurs on evoking the Poincaré-Brouwer theorem[70]. This theorem was originally proven by Poincaré and is sometimes called the hairy-ball theorem; it states that there exists at least one point on the surface of a sphere at which vectors of electric and magnetic fields become equal to zero. The Poynting vector is also zero at this point. This theorem indicates a toroidal shape instead of a spherical circulator, which is the second lesson from nature about solar light harvesting[7], but which is unfortunately violated in a recent design of bio-inspired optical antennae[71].



#### 4. Discussion

The subtlety in the structures arises in whether the LH comprise overlapping rings or non-overlapping rings. The vigilant reader might recognize that we consider them as overlapping in the case of small-loop antennae but non-overlapping when discussing non-reciprocity. The same issue governs the problems of quantum or not quantum (classical), conductor or not conductor (dielectric). Simplification gives insight, which is the key to our discovery and which is a major approach of physicists[72].

The analysis in Section 2 considers the antenna to be a conductor whereas chlorophylls are dielectric. Dielectric can be used to build antennae, which was invented in 1939, tested in 1982, and is now widely used in optical communication[73, 74, 75]. For the frequency of sunlight, a metal becomes lossy; a dielectric works better. Furthermore, dielectric receivers immunize the antennae from damage due to high power[76, 77], which is generally attributed to the carotenoids involved, but carotenoids are missing in the FMO complex[78]. In the last three decades various shape have been considered[79]. A ring (or shell) shape dielectric antenna or a four-elements cylindrical dielectric antenna with centre feed resemble our light-harvesting system[80]. The antenna must work with symmetry breaking of the electric field in space to function[81], which is the second reason for the mysterious opening. When the sunlight (an electromagnetic wave) excites a resonance in the antenna, a mode field pattern is built up inside the structure. The location of each module of chlorophyll corresponds to the mode of the electric field of the antenna, although previous authors failed to realize that these are mimicking nature[82, 79].

The primary step of photosynthesis, which includes energy transfer and electron transfer[83], to the special pair of the RC, i.e. the energy-transfer part of the primary step of photosynthesis, is explicable presumably in terms of classical electrodynamics. Recent research confirmed this point of view[33]. After the special pair, as the light (wave) has transferred into an electron (particle), we must consider quantum mechanics, for which reason a special pair is a dimer instead of a trimer. The special pair resembles two optical fibres of a lately realized nano-circulator[40]. Nature is playing football at the light harvester with the electron being the football.

There are systems with more sophisticated symmetries, i.e. symmetry D3 of red-shifted phycobiliprotein complexes isolated from the chlorophyll f-containing cyanobacterium *Halomicronema hongdechloris*[84]; C-Phycocyanin from *Leptolyngbya*[85], and C-phycoerythrin from cyanobacterium *Phormidium*[86]. Symmetry D3 represents a twisted or a stereo symmetry C3. Furthermore, the number of bacteriochlorophylls in each module might be another level of symmetry: first, it means self-similarity as discussed in fractal theories[87], second, the number three instead of two, like the special pair in the RC, might indicate classical instead of quantum. For the same reason, photosystems I and photosystems II of algae and plants should evolve from the same principle, although equipped with more sophisticated material.

In summary, in this work, we sought another possibility to consider a light-

harvesting antenna as a device to receive electromagnetic waves. We find that a modular LH is an effective design to make an antenna receive more than it emits. Our model from classical electrodynamics has the structural information enforced. We thereby provide an explanation for

1. the function of the notch,
2. the non-heme iron at the LH1-RC complex,
3. the reason for use of dielectric chlorophylls as an antenna,
4. a mechanism to prevent damages from excess sunlight,
5. the wavelike energy transfer observed,
6. the physics behind photon anti-bunching.

We show that both physics and chemistry illuminate the problem of photosynthesis. All four categories of non-reciprocity and dielectric resonator antennae deserve further investigation. As the geometry is known, we interpret its mechanism that might be useful for the future production of artificial light-harvesting systems[7, 88, 89].

## References

- [1] R. S. Knox, *Photosynth. Res.* **48**, 35 (1996).
- [2] D. Voet and J. Voet, *Biochemistry*, John Wiley & Sons, Hoboken, 4 edition, 2011.
- [3] J. M. Berg, J. L. Tymoczko, L. Stryer, G. J. Gatto, and L. Stryer, *Biochemistry*, W.H. Freeman, New York, 8 edition, 2015.
- [4] N. Lambert et al., *Nat. Phys.* **9**, 10 (2012).
- [5] R. van Grondelle and H. van Gorkom, *Photosynth. Res.* **120**, 3 (2014).
- [6] R. E. Fenna and B. W. Matthews, *Nature* **258**, 573 (1975).
- [7] G. D. Scholes, G. R. Fleming, A. Olaya-Castro, and R. van Grondelle, *Nat. Chem.* **3 VN - re**, 763 (2011).
- [8] J. Deisenhofer, O. Epp, K. Miki, R. Huber, and H. Michel, *J. Mol. Biol.* **180**, 385 (1984).
- [9] W. Kühlbrandt, *Nature* **374**, 497 (1995).
- [10] X. Hu and K. Schulten, *Phys. Today* **50**, 28 (1997).
- [11] R. J. Cogdell, A. Gall, and J. Köhler, *Q. Rev. Biophys.* **39**, 227 (2006).
- [12] S. Karrasch et al., *EMBO J.* **14**, 631 (1995).
- [13] S. E. Bradforth, R. Jimenez, F. van Mourik, R. van Grondelle, and G. R. Fleming, *J. Phys. Chem.* **99**, 16179 (1995).

- [14] G. McDermott et al., *Nature* **374**, 517 (1995).
- [15] M. Z. Papiz, S. M. Prince, T. Howard, R. J. Cogdell, and N. W. Isaacs, *J. Mol. Biol.* **326**, 1523 (2003).
- [16] K. Holden-Dye, L. I. Crouch, and M. R. Jones, *Biochim. Biophys. Acta - Bioenerg.* **1777**, 613 (2008).
- [17] J. C. Newman and A. Weiner, *Mol. Cell* **10**, 437 (2002).
- [18] R. J. Cogdell et al., *J. Bacteriol.* **181**, 3869 (1999).
- [19] K. McLuskey, S. M. Prince, R. J. Cogdell, and N. W. Isaacs, *Biochemistry* **40**, 8783 (2001).
- [20] A. W. Roszak, *Science* (80-. ). **302**, 1969 (2003).
- [21] J. Koepke, X. Hu, C. Muenke, K. Schulten, and H. Michel, *Structure* **4**, 581 (1996).
- [22] E. Hofmann et al., *Science* (80-. ). **272**, 1788 LP (1996).
- [23] D. E. Tronrud, J. Wen, L. Gay, and R. E. Blankenship, *Photosynth. Res.* **100**, 79 (2009).
- [24] R. R. Sonani, G. D. Gupta, D. Madamwar, and V. Kumar, *PLoS One* **10**, e0124580 (2015).
- [25] T. Foerster, *Naturwissenschaften* **33**, 166 (1948).
- [26] L. N. Duysens, *Brookhaven Symp. Biol.* **11**, 10 (1959).
- [27] E. W. Montroll, *J. Math. Phys.* **10**, 753 (1969).
- [28] S. G. Liu et al., *Science* (80-. ). **316**, 1462 LP (2007).
- [29] S. Lloyd, *Nat. Phys.* **5**, 164 (2009).
- [30] M. Mohseni, P. Rebentrost, S. Lloyd, and A. Aspuru-Guzik, *J. Chem. Phys.* **129**, 0 (2008).
- [31] et al. S. Gregory et al., *Nature* **446**, 782 (2007).
- [32] M. O. Scully, K. R. Chapin, K. E. Dorfman, M. B. Kim, and A. Svidzinsky, *Proc. Natl. Acad. Sci.* **108**, 15097 (2011).
- [33] K. E. Dorfman, D. V. Voronine, S. Mukamel, and M. O. Scully, *Proc Natl Acad Sci U S A* **110**, 2746 (2013).
- [34] J. J.-L. Ting, *Eur. Phys. J. B* **12**, 163 (1999).
- [35] J. D. Kraus, *Antenna*, McGraw-Hill, New York USA, 2 edition, 1988.

- [36] R. E. Collin, *Foundations for microwave engineering*, IEEE Press, New York, 2001.
- [37] D. Jalas et al., Nat Phot. **7**, 579 (2013).
- [38] M. Faraday, *Experimental researches in electricity*, R. and J. E. Taylor, London, 1839.
- [39] B. E. A. Saleh and M. C. Teich, *Fundamentals of Photonics*, Wiley, 2 edition, 2007.
- [40] M. Scheucher, E. Will, and A. Rauschenbeutel, Science (80-. ). **354**, 1577 (2016).
- [41] H. Lira, Z. Yu, S. Fan, and M. Lipson, Phys. Rev. Lett. **109**, 1 (2012).
- [42] L. D. Tzuang, K. Fang, P. Nussenzveig, S. Fan, and M. Lipson, Nat Phot. **8**, 701 (2014).
- [43] J. Kim, M. C. Kuzyk, K. Han, H. Wang, and G. Bahl, Nat Phys **11**, 275 (2015).
- [44] S. Lepri and G. Casati, Phys. Rev. Lett. **106**, 1 (2011).
- [45] A. M. Mahmoud, A. R. Davoyan, and N. Engheta, Nat. Commun. **6**, 8359 (2015).
- [46] M. Krause, H. Renner, and E. Brinkmeyer, Electron. Lett. **44**, 691 (2008).
- [47] C. G. Poulton et al., Opt. Express **20**, 21235 (2012).
- [48] M. D. Tocci, M. J. Bloemer, M. Scalora, J. P. Dowling, and C. M. Bowden, Appl. Phys. Lett. **66**, 2324 (1995).
- [49] K. Gallo, G. Assanto, K. R. Parameswaran, and M. M. Fejer, Appl. Phys. Lett. **79**, 314 (2001).
- [50] J. P. Allen, G. Feher, T. O. Yeates, H. Komiya, and D. C. Rees, Proc. Natl. Acad. Sci. U. S. A. **84**, 5730 (1987).
- [51] C. Kirmaier and D. Holten, Proc. Natl. Acad. Sci. USA **83**, 6407 (1986).
- [52] J. Deisenhofer and J. R. Norris, *The Photosynthetic reaction center*, Academic Press, San Diego, CA, 1993.
- [53] G. L. Miessler et al., *Inorganic Chemistry*, Pearson Education, Inc., 5 edition, 2008.
- [54] G. A. Lawrance, *Introduction to Coordination Chemistry*, John Wiley & Sons, Ltd, Chichester, UK, 2010.
- [55] S. Hermes et al., Biochemistry **45**, 353 (2006).

- [56] T. M. Nordlund, *Quantitative understanding of biosystems : an introduction to biophysics*, Taylor & Francis, Boca Raton, 2011.
- [57] S. Vandendriessche, V. K. Valev, and T. Verbiest, Phys. Chem. Chem. Phys. **14**, 1860 (2012).
- [58] S. Vandendriessche et al., Chem. Mater. **25**, 1139 (2013).
- [59] C. Sayrin et al., Phys. Rev. X **5**, 041036 (2015).
- [60] F. Müh and A. Zouni, Photosynth. Res. **116**, 295 (2013).
- [61] A. Y. Semenov, V. N. Kurashov, and M. D. Mamedov, J. Photochem. Photobiol. B Biol. **104**, 326 (2011).
- [62] A. Ishizaki and G. R. Fleming, Proc. Natl. Acad. Sci. U. S. A. **106**, 17255 (2009).
- [63] E. Romero et al., Nat. Phys. **10**, 676 (2014).
- [64] T. P. J. Krüger et al., Proc. Natl. Acad. Sci. U. S. A. **108**, 13516 (2011).
- [65] E. Wientjes et al., Nat. Commun. **5**, 4236 (2014).
- [66] F. Pérez-Cota et al., Sci. Rep. **6**, 1 (2016).
- [67] Y. Zhuo et al., Prog. Quantum Electron. **50**, 1 (2016).
- [68] G. I. Barenblatt, *Scaling*, Cambridge University Press, Cambridge, 2003.
- [69] O. Hassan Omar et al., Bioconjug. Chem. **27**, 1614 (2016).
- [70] L. E. J. Brouwer, Math. Ann. **71**, 97 (1911).
- [71] S. Hong, M. Y. Lee, A. O. Jackson, and L. P. Lee, Light Sci. Appl. **4**, e267 (2015).
- [72] S. M. Gruner, J. S. Langer, P. Nelson, and V. Vogel, Phys. Today **48**, 25 (1995).
- [73] R. D. Richtmyer, J. Appl. Phys. **10**, 391 (1939).
- [74] S. A. Long, M. W. McAllister, L. C. Shen, and Liang Shen, IEEE Trans. Antennas Propag. **AP-31**, 406 (1983).
- [75] K.-C. Huang and D. J. Edwards, *Millimetre wave antennas for gigabit for wireless communications : a practical guide to design and analysis in a system Context*, John Wiley & Sons, New Jersey, 2008.
- [76] R. C. J. Hsu, A. Ayazi, B. Houshmand, and B. Jalali, IEEE MTT-S Int. Microw. Symp. Dig. **16**, 221 (2007).
- [77] R. C. J. Hsu, A. Ayazi, B. Houshmand, and B. Jalali, Nat Phot. **1**, 535 (2007).

- [78] R. J. Cogdell et al., Philos. Trans. R. Soc. B Biol. Sci. **355**, 1345 (2000).
- [79] D. Soren, R. Ghatak, R. K. Mishra, and D. R. Poddar, Prog. Electromagn. Res. B **60**, 195 (2014).
- [80] D. Guha and Y. Antar, IEEE Trans. Antennas Propag. **54**, 2657 (2006).
- [81] D. Sinha and G. A. J. Amaratunga, Phys. Rev. Lett. **114**, 147701 (2015).
- [82] Y. Yu, V. E. Ferry, A. P. Alivisatos, and L. Cao, Nano Lett. **12**, 3674 (2012).
- [83] G. R. Fleming and R. V. Grondelle, Phys. Today **47**, 48 (1994).
- [84] Y. Li et al., Biochim. Biophys. Acta - Bioenerg. **1857**, 107 (2016).
- [85] N. K. Singh et al., CNS Neurol. Disord. - Drug Targets **13**, 691 (2014).
- [86] V. Kumar, R. R. Sonani, M. Sharma, G. D. Gupta, and D. Madamwar, Photosynth. Res. **129**, 17 (2016).
- [87] B. Mandelbrot, Science (80-. ). **156**, 636 LP (1967).
- [88] Y. Yu and L. Cao, Opt. Commun. **314**, 79 (2014).
- [89] T. P. J. Krüger and R. van Grondelle, Phys. B Condens. Matter **480**, 7 (2016).